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The chromosomes of *Gazella bennetti* and *Gazella saudiya*

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Abstract

Seven individuals of captive *Gazella bennetti* were found to have chromosomal complements of 2n = 49–52, and seven captive *G. saudiya* had complements of 2n = 46–53. G-banded karyotypes revealed that variation in diploid number was the result of an autosome-to-X chromosome translocation and four independent Robertsonian translocations. There were no fixed chromosomal differences between *G. bennetti* and *G. saudiya*, but two pericentric inversions distinguished Pakistani *G. bennetti* from Iranian *G. bennetti* and *G. saudiya*. Several pairs of metacentric chromosomes of both species were monobrachially homologous with metacentrics of *G. dorcas* and *G. gazella*, indicating *G. bennetti* and *G. saudiya* are reproductively isolated from *G. dorcas* and *G. gazella*. As with other species of gazelles, chromosomal studies of natural populations are needed for these species.

Introduction

Gazelles (genus *Gazella*) occur in arid and semi-arid habitats from northern Africa to central Asia. Sixteen species make *Gazella* one of the most diverse genera of artiodactyls (Grubb 1993). Ability to exploit a variety of niches in a stressful environment with few competitors has enhanced the radiation of gazelles. As a result of their diversification, the taxonomy of gazelles is complicated and uncertain (Groves 1988), particularly with regard to the Indian gazelle, *G. bennetti*, and the Saudi gazelle, *G. saudiya*. Ellerman and Morrison-Scott (1951) considered *bennetti* a subspecies of the mountain gazelle, *G. gazella*, and *saudiya* was treated as a subspecies of the dorcas gazelle, *G. dorcas*. Based on skull measurements, both *bennetti* and *saudiya* were placed with *G. dorcas* by Groves (1969) and Lange (1972). More recently, *G. bennetti* and *G. saudiya* have been recognized as distinct species (Groves 1988).

Chromosomal data suggest that *bennetti* and *saudiya* are not conspecific with *G. gazella* or *G. dorcas*. The chromosomal complements of *G. dorcas* and *G. gazella*, respectively, are 2n = 30, 31 (♀, ♂) and 2n = 34, 35 (Hsu and Benirschke 1967/77; Wurster 1972, Wahrman et al. 1973; Effron et al. 1976; Kingswood and Kumamoto 1988; Vassart 1994). Previous investigations have found chromosomal complements of 2n = 50, 51 in *G. bennetti* (Furley et al. 1988) and 2n = 47, 50–51 in *G. saudiya* (Rebholz et al. 1991). These investigations presented nondifferentially-stained karyotypes and, in the case of *G. bennetti*, C-banded chromosomes. With G-banding however, it is possible to determine the extent of chromosomal homology between taxa. The present cytogenetic study documents nondifferentially-stained, C-banded, and G-banded karyotypes of captive *G. bennetti* and *G. saudiya*. These data are compared with G-banded karyptypes of *G. dorcas* and *G. gazella* in order to delineate chromosomal relationships among these four gazelles.

Material and methods

Seven specimens of *G. bennetti* (5♀♀, 2♂♂), seven *G. saudiya* (5♀♀, 2♂♂), two *G. dorcas* (2♂♂), and two *G. gazella* (1♀, 1♂) were examined, all of them belonging to captive populations at Al-Areen Wildlife Park (Bahrain), Al-Wabra (Qatar), and King Khalid Wildlife Research Center (Saudi Arabia). Origins of the *saudiya* individuals were uncertain, but they were likely from an introduced island population off the northern coast of Qatar that was established with animals from different locales on the mainland (F. Al-Timimi, pers. comm.; East 1992). The *bennetti* specimens apparently originated from Iran and Pakistan, but their exact geographic origins were unknown. The *dorcas* individuals were apparently from Sudan, but origin of the *gazella* specimens were unknown.

Specimens of the four gazelle taxa were phenotypically distinguishable on the basis of characteristics described by Groves (1988). Horns of the *bennetti* and *saudiya* were long, straight and well-formed in both sexes while horns of the *dorcas* and *gazella* were shorter by comparison. The male Indian gazelles differed from the Saudi gazelles by having horns that were distinctly ringed. Horns of the dorcas gazelles were S-shaped and curved inward at the tips; horns in the male mountain gazelle were stout but were delicate in the female. Pelage characteristics included differences in the development of body and facial stripes. Body markings were nearly absent in the specimens of *saudiya*, poorly developed in the *bennetti* (both body and facial stripes), a poorly marked flank stripe but well-marked facial stripes in the *dorcas*, and well-marked flank and facial stripes in the *gazella*.

Heparinized whole blood (5–10 ml) and/or skin biopsies (ca. 5 mm^2) were collected for cell culture and transported to the Conservation Genetics Laboratory of the Zoological Society of London. Short-term lymphocyte culture followed a modified technique of Moorhead et al. (1960) and Wiley and Meisner (1984) using pokeweed mitogen (0.3 ml) and co-mitogen phorbol 12-myristate 13-acetate-4-0-methyl ether (final concentration 6 mcg/ml). Blood cultures were harvested at 94 h and after a 1 h exposure to colcemid (final concentration 0.025 mcg/ml). Skin biopsies were processed for fibroblast cell culture using a collagenase-disaggregation technique. Cell harvest followed the general protocol for monolayer cultures (Barch 1991). At peak mitotic activity, monolayer cultures were exposed to colcemid (final concentration 0.025 mcg/ml) for 10–30 min, and cells were then exposed to 0.075 M KCl for 10 min prior to fixation of cells.

G-band, C-band, and nondifferentially-stained preparations were prepared from the mitotic cell harvests. G-banding followed Verma and Babu (1989), and C-banding followed Sumner (1972). Because of the difficulty in comparing G-band homologies between taxa without a standardized nomenclature, G-banded chromosomes were numbered according to the standard karyotype of cattle, *Bos taurus*, presented by Ford et al. (1980) and Iannuzzi (1990). Gallagher and Womack (1992) demonstrated extensive arm homologies among several species of bovids using the cattle standard. Because chromosome-arm homologies between the karyotypes of gazelles and cattle were extensive, we referenced gazelle chromosomes strictly by cattle homology to facilitate comparisons between our specimens. (Note: chromosome 3 of *B. taurus* differed from chromosome 3 of the gazelles by a paracentric inversion.) Thus, assignment of different numbering systems to the karyotypes of each species was avoided. Robertsonian fusions that were polymorphic are indicated in parentheses to distinguish them from fusions that were fixed.

Results

The chromosomal complement of *G. saudiya* was 2n = 46–53, and *G. bennetti* was 2n = 49–52 (Tab. 1). All specimens possessed an autosome-to-X translocation; thus, one element of pair 5 occurred as an additional acrocentric autosome in males (Figs. 1, 2). Four independent Robertsonian (Rb) translocations were polymorphic in *saudiya* with seven different karyotypic configurations. Three independent Robertsonian translocations were polymorphic in Iranian *bennetti* while Pakistani *bennetti* was polymorphic only for Rb(8;14). Pakistani specimens could also be distinguished from *saudiya* and Iranian *bennetti* by two pericentric inversions in the small autosomal pairs 22 and 25. The difference

Table 1. Summary of chromosomal data for *G. saudiya* and *G. bennetti*

Case no.	Sex	2n	NAA	(4;12)	(8;14)	(9;23)	(11;17)	22	25
G. saudiya									
8349	♀	46	60	X	XX	X	XX	m	m
8348	♀	48	60	–	XX	X	X	m	m
8358	♀	49	60	–	XX	X	–	m	m
8346	♂	49	61	–	X	X	XX	m	m
8350	♀	50	60	X	–	X	–	m	m
8347	♀	50	60	–	X	X	–	m	m
8351	♂	53	61	–	–	–	–	m	m
G. bennetti (Iran)									
8339	♂	49	61	–	XX	X	X	m	m
8338	♀	52	60	–	–	–	–	m	m
G. bennetti (Pakistan)									
8342	♀	50	56	–	XX	–	–	a	a
8340	♀	51	56	–	X	–	–	a	a
8344	♀	51	56	–	X	–	–	a	a
8345	♀	51	56	–	X	–	–	a	a
8341	♂	52	57	–	X	–	–	a	a

2n = diploid number, NAA = autosomal arm number, (4;12), (8;14), (9;23) and (1;17) = Robertsonian translocations, 22 and 25 = autosomal pairs rearranged by pericentric inversion, XX = translocation homozygous, X = translocation heterozygous, – = translocation not carried, m = metacentric, a = acrocentric

in autosomal arm number between the two groups was due to metacentric versus acrocentric forms of pairs 22 and 25 in Iranian and Pakistani specimens, respectively. The inversion polymorphisms were difficult to detect in G-banded karyotypes because of the small size of the chromosomes, but were obvious in nondifferentially-stained and C-banded karyotypes.

Taking the various rearrangements into account, comparison of G-bands among the 14 specimens of *bennetti* and *saudiya* revealed consistent band patterns (Figs. 1, 2), and 17 chromosomal pairs were homologous (Tab. 2). Autosomes were G-band negative around the centromere, corresponding to lightly-stained C-band positive regions. Acrocentric autosomes of both taxa had tiny p-arms (short arms) and size polymorphisms were evident in some of the pairs; particularly in pairs 1, 3, 7, and 18. Autosomes exhibited pericentromeric heterochromatin, but the degree to which they stained for heterochromatin was not consistent. The X chromosomes of *bennetti* and *saudiya* were large submetacentric elements with identical G-banding patterns and autosome 5 fused to the q-arm (long arm) of the X chromosome. The short arm of the X was polymorphic in size and was heterochromatic. The Y chromosomes of both taxa were submetacentric with identical G-banding patterns, and they appeared heterochromatic by C-banding. Taking into account chromosomal differences between males and females, the karyotypes of a male Iranian *bennetti* (2n = 49, case no. 8339) and a female *saudiya* (2n = 48, case no. 8348) were identical, as were the karyotypes of a female Iranian *bennetti* (2n = 52, case no. 8338) and a male *saudiya* (2n = 53, case no. 8351) (Figs. 1, 2).

Comparison of G-banded karyotypes of *bennetti* and *saudiya* with those of *dorcas* and *gazella* (Fig. 3), indicated autosome 5 was the only element unchanged among the four taxa (Tab. 2). Chromosome 5 was involved in the autosome-to-X translocations of all four species. Rb(8;14) was polymorphic in *bennetti* and *saudiya* but was fixed in *dorcas* and *ga-*

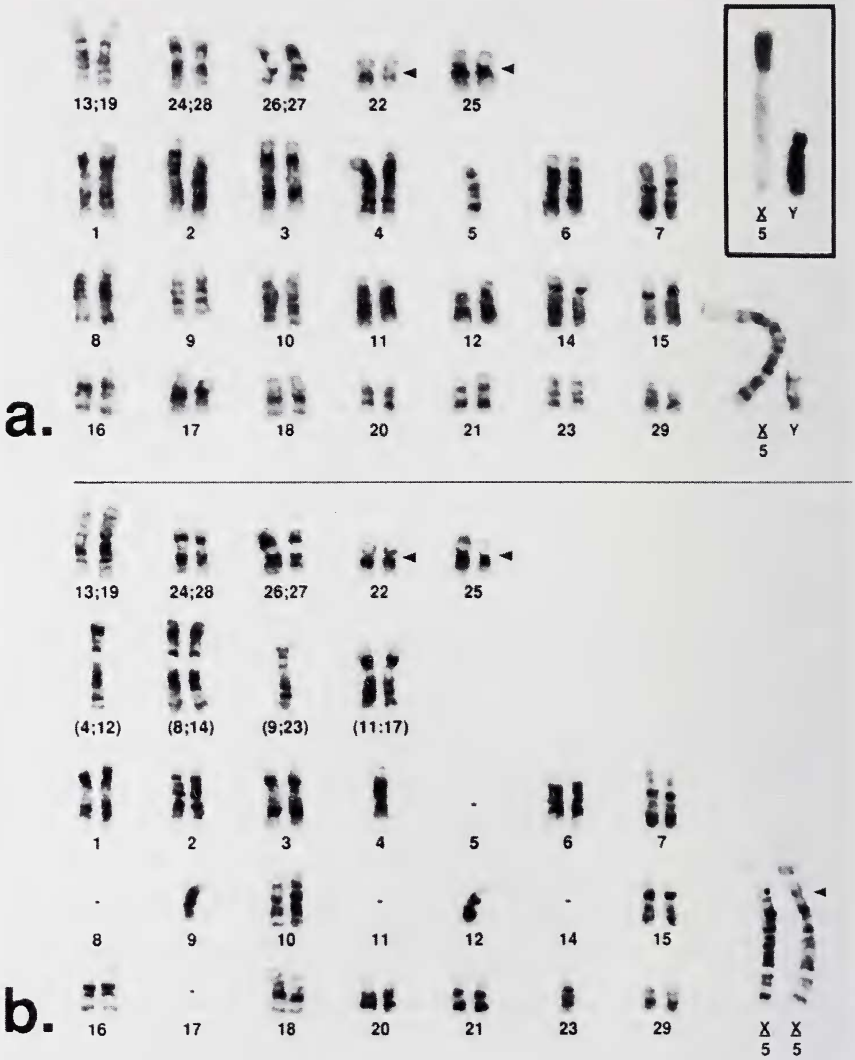

Fig. 1. G-banded karyotypes of *G. saudiya*: *a*–male 2n = 53 (case no. 8351); *b*–female 2n = 46 (case no. 8349). Boxed inset: C-banded sex chromosomes. Arrowhead indicates centromere position.

zella. Pairs 20, 21, and 29 were conserved among *bennetti*, *saudiya*, and *gazella* but were rearranged in *dorcas*. Between *bennetti*/*saudiya* and *dorcas*/*gazella*, all other chromosomes were rearranged. There were 9 monobrachially homologous metacentrics among *bennetti* and *gazella*, 10 among *bennetti* and *dorcas*, 11 among *saudiya* and *gazella*, and 12 among *saudiya* and *dorcas*. Ten metacentric pairs and one acrocentric pair were conserved between the karyotypes of *dorcas* and *gazella* (Tab. 2). These two species were distinguishable from each other by one Robertsonian translocation (Rb 20;29) and three monobrachially homologous metacentrics in *dorcas* (2;24, 21;23, and 25;28) and two in *gazella* (2;25 and 23;24). Acrocentric chromosome 28 in *gazella* was single-arm homologous to *dorcas* metacentric 25;28.

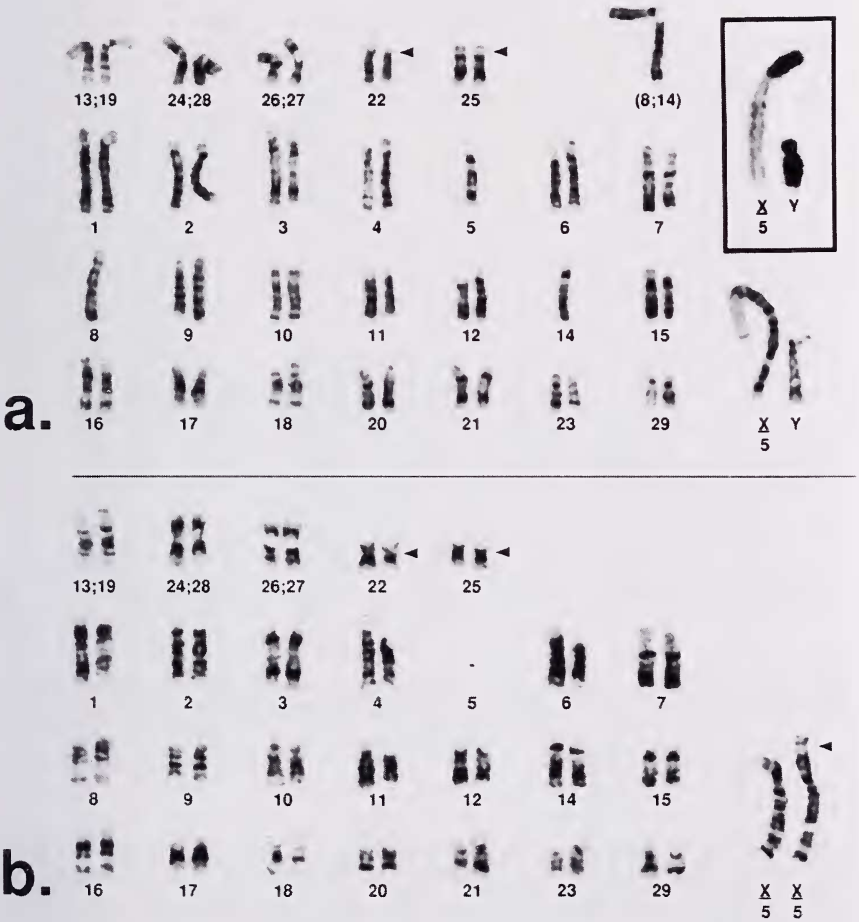

Fig. 2. G-banded karyotypes of *G. bennetti*: *a*–male 2n = 52 (case no. 8 341); *b*–female 2n = 52 (case no. 8 338). Boxed inset: C-banded sex chromosomes. Arrowhead indicates centromere position.

Table 2. Conserved and rearranged autosomes for *G. saudiya*, *G. bennetti*, *G. gazella*, and *G. dorcas*

	G. saudiya		*G. bennetti*		*G. gazella*		*G. dorcas*
CONSERVED AUTOSOMES	5	=	5	=	5	=	5
	(8;14)	=	(8;14)	=	8;14	=	8;14
	20	=	20	=	20		–
	21	=	21	=	21		–
	29	=	29	=	29		–
	1	=	1		–		–
	2	=	2		–		–
	3	=	3		–		–
	6	=	6		–		–
	7	=	7		–		–
	10	=	10		–		–
	15	=	15		–		–
	16	=	16		–		–
	18	=	18		–		–
	20	=	20		–		–
	(9;23)*	=	(9;23)*		–		–
	(11;17)*	=	(11;17)*		–		–
	13;19*	=	13;19*		–		–
	24;28*	=	24;28*		–		–
	26;27*	=	26;27*		–		–
	–		–		1;10	=	1;10
	–		–		3;27	=	3;27
	–		–		4;7	=	4;7
	–		–		6;19	=	6;19
	–		–		9;12	=	9;12
	–		–		11;18	=	11;18
	–		–		13;15	=	13;15
	–		–		16;22	=	16;22
	–		–		17;26	=	17;26
REARRANGED AUTOSOMES							
Pericentric inversions	22	inv	(22)		–		–
	25	inv	(25)		–		–
Robertsonian translocation	(4;12)*	Rb	4 and 12		–		–
	–		–		–	Rb	20;29
Monobrachial homologs	–		–		2;25		2;24
	–		–		23;24		21;23
	–		–		28		25;28

Autosomes in parentheses were polymorphic. Metacentric autosomes of *G. saudiya* and *G. bennetti* that were monobrachially homologous with metacentrics of *G. gazella* or *G. dorcas* are marked with an asterisk.

While the sex chromosomes of *bennetti* and *saudiya* were identical, differences were found between those of *dorcas* and *gazella*. The X chromosome of *gazella* was a large submetacentric with autosome 5 fused to the distal end, but a small pericentric inversion differentiated it from the X of *bennetti* and *saudiya*, such that in *gazella*, a G-band positive band appeared in the p-arm adjacent to the centromere (Fig. 3 b). Like *bennetti* and *saudiya*, the Xp of *gazella* was polymorphic in size and entirely heterochromatic, however, in *gazella* a single light interstitial C-band positive band was apparent on the Xq (Fig. 3 b). The X chromosome of *dorcas* was a large acrocentric element, homologous to Xq of *bennetti* and *saudiya*. The pericentromeric region of the *dorcas* X was C-band positive (Fig. 3 a). The Y chromosome of *dorcas* was a tiny metacentric element.

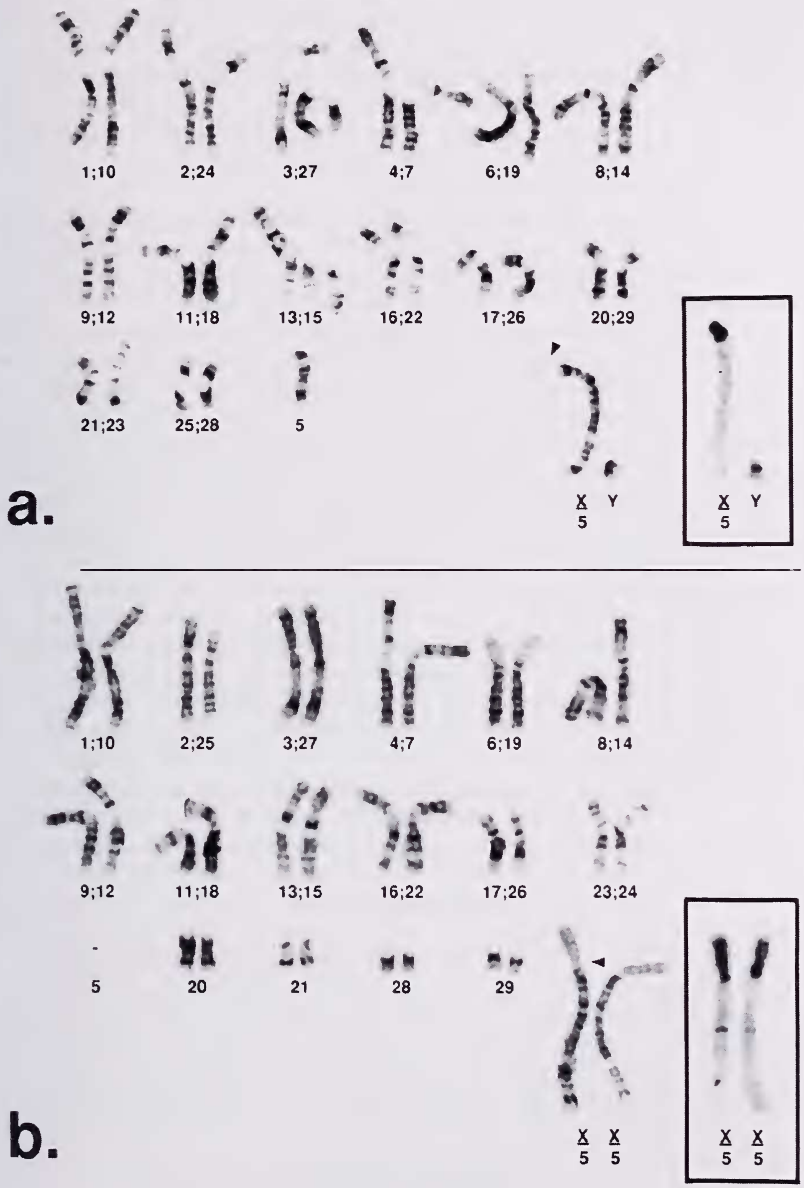

Fig. 3. *a*–G-banded karyotype of a male *G. dorcas* 2n = 31 (case no. 8 334); *b*–G-banded karyotype of a female *G. gazella* 2n = 34 (case no. 8 319). Boxed insets: C-banded sex chromosomes. Arrowhead indicates centromere position.

Discussion

Chromosomal complements of 2n = 49–52 in *G. bennetti* and 2n = 46–53 in *G. saudiya* found in this study are consistent with previous reports of 2n = 50, 51 and 2n = 47, 50–51, respectively, for the two species (Furley et al. 1988; Rebholz et al. 1991). It is worth noting that none of the gazelles karyotyped here were the same individuals as described in the previous reports. These data contrast remarkably with complements of 2n = 30, 31 in *G. dorcas* and 2n = 34, 35 in *G. gazella* (Hsu and Benirschke 1967/77; Wurster 1972; Wahrman et al. 1973; Effron et al. 1976; Kingswood and Kumamoto 1988; Vassart 1994). Despite the chromosomal differences, the autosome translocated to the X chromosome is the same element in all four taxa and in seven other species of gazelles, as well as in *Antilope cervicapra* (Vassart 1994), suggesting the autosome-to-X translocation occurred only once during the evolution of gazelles.

G-banded karyotypes demonstrate extensive monobrachial homology between metacentric chromosomes of *bennetti* and *saudiya* on the one hand, and *dorcas* and *gazella* on the other. Monobrachial centric fusions are believed to have been fundamental in the chromosomal evolution of gazelles and other bovid taxa (Effron et al. 1976; Gallagher and Womack 1992) and are thought to effect reproductive isolation (Baker and Bickham 1986). The extent to which multiple Robertsonian rearrangements potentially reduce fertility and effect reproductive isolation has been demonstrated in gazelles. Wahrman et al. (1973) reported that when captive *dorcas* and *gazella* hybridized, male offspring were sterile and female hybrids had reduced fertility. Five metacentric pairs were monobrachially homologous among the *dorcas* and *gazella* in our study. Although we have no direct information regarding the consequences of crossing either *bennetti* or *saudiya* with *dorcas* or *gazella*, the monobrachial rearrangements distinguishing their karyotypes indicate they are reproductively isolated. Thus, chromosomal data support the suggestion by Groves (1988) that *bennetti* and *saudiya* are not conspecific with either *dorcas* or *gazella*.

While cytogenetic data clearly indicate that neither *bennetti* nor *saudiya* are conspecific with *dorcas* or *gazella*, chromosomal differences between *bennetti* and *saudiya* are less obvious. The only chromosomal rearrangement that could be used to distinguish *bennetti* from *saudiya* was the 4;12 translocation carried by two specimens of *saudiya*. If specimens of *saudiya* did not carry the 4;12 translocation, however, karyotypic differences between individual specimens were not definitive for either taxon. Taking into account chromosomal differences between females and males, G-banded karyotypes of two specimens of *bennetti* could not be distinguished from those of two *saudiya*. There were no fixed chromosomal differences between *bennetti* and *saudiya* and, more importantly, there were no monobrachial homologues. Thus, our data indicate that *bennetti* and *saudiya* are not cytogenetically distinct. This finding is consistent with the review of Corbet (1978), insofar as both taxa have been regarded as subspecies of *dorcas*, and the suggestion by Furley et al. (1988) that *bennetti* and *saudiya* might form a taxonomic complex.

The uncertain geographical origin of our panel of specimens makes it difficult to draw conclusions about taxonomic relationships between *bennetti* and *saudiya*. Based on differences between the karyotypes of three specimens of *saudiya* (2n = 47, 50, and 51), Rebholz et al. (1991) suggested that their group might have represented hybrids. Our panel of *saudiya* did not include individuals studied by Rebholz et al. (1991), but it represented the same captive populations (Al-Areen Wildlife Park and King Khalid Wildlife Research Center). Just as in the earlier study, the karyotypes of all seven *saudiya* in our study were different from each other. If hybridization with *bennetti* occurred, as a result of mixing both taxa on an island or in captivity, it may be that historical populations of *saudiya* had chromosomal numbers closer to 2n = 46 and 47 than to the 2n = 49–52, and possibly 53, of *bennetti*. On the other hand, Benirschke et al. (1984) raised the possibility that the karyotypic variability (three independent Robertsonian polymorphisms) observed in captive

G. soemmerringi might not be the result of hybridization with related species but may, instead, be correlated with different subspecies. Thus, the possibility cannot be ruled out that chromosomal polymorphisms occurred naturally in different populations of *saudiya*.

Questions regarding hybridization in *saudiya* raises the possibility that our panel of *bennetti* also included hybrids. Chromosomal data for the five Pakistani animals are consistent with data for the three animals studied by FURLEY et al. (1988), also from Pakistan. Our Pakistani specimens were distinguishable from *saudiya*, and Iranian *bennetti*, by two pericentric inversions. If there were hybrids among our panel of Pakistani *bennetti*, inversion heterozygotes would have been expected. However, cytogenetic similarities between two Iranian *bennetti* and two *saudiya* leave open the possibility that the so-called Iranian specimens might be hybrids.

Another possibility suggested by the occurrence of the same translocation polymorphisms in *saudiya* and Iranian *bennetti* is that gene flow between their populations has prevented the fixation of different chromosomal rearrangements. The pericentric inversions that distinguish these two taxa from Pakistani *bennetti*, however, appear to be fixed. Populations of *bennetti* in the Seistan and Thar deserts are thought to be separated be either the Indus river or the edge of the Iranian plateau (GROVES 1969). Assuming that our Iranian *bennetti* represent the Seistan population (*G. b. fuscifrons*) and that Pakistani specimens are from the Thar population (*G. b. christii*), it is possible that the chromosomal differences observed in captive *bennetti* reflect these natural populations and are the result of their geographic isolation. However, uncontrolled transport of live gazelles throughout the Middle East for the pet trade adds to the difficulty of making inferences about the origin and taxonomic status of any captive specimens (FURLEY et al. 1988).

Cytogenetic studies of gazelles across their natural geographic range are urgently needed to define the occurrence of intraspecific chromosomal variation that has been documented in captive populations. Although *G. bennetti* has been greatly reduced in numbers or eliminated from many areas, it still occurs locally in good numbers from central Iran to central India (EAST 1993). Unfortunately, *G. saudiya* is believed to be extinct in the wild (GROOMBRIDGE 1993) so it is unlikely that karyotypes of natural populations will ever be known. Thus, chromosomal studies of captive and introduced populations of *saudiya* have added significance in terms of conservation and breeding efforts, particularly since intraspecific chromosomal variation represents a potential threat to reproduction (for reviews see BENIRSCHKE and KUMAMOTO 1991; ROBINSON and ELDER 1993). Therefore, cytogenetic studies should include evaluations of the effects that chromosomal polymorphisms have on the fertility of these threatened species.

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Zusammenfassung

Die Chromosomen von Gazella bennetti und Gazella saudiya

Sieben in Gefangenschaft gehaltene Gazellen der Art *Gazella bennetti* hatten eine Chromosomenzahl von 2n = 49–52, und sieben *G. saudiya* hatten 2n = 46–53. Die Giemsa Bandmuster der Chromosomen

zeigten, daß die Variation der diploiden Chromosomenzahl zum Teil auf die Autosom/X-Chromosomen Translokation, und zum Teil auf vier unabhängige Robertsonische Translokationen von Autosomen zurückzuführen ist. Keine beständigen Chromosomenunterschiede bestanden zwischen *G. bennetti* und *G. saudiya*, hingegen unterschied sich *G. bennetti* von Pakistan von *G. bennetti* aus Iran und *G. saudiya*, durch zwei perizentrische Inversionen. Mehrere der metazentrischen Autosomen beider Arten hatten monobrachiale Homologie mit metazentrischen Autosomen von *G. dorcas* und *G. gazella*. Dieser Befund beweist, daß *G. bennetti* und *G. saudiya* von *G. dorcas* und *gazella* reproduktiv isoliert sind. Wie es auch für andere Gazellenarten der Fall ist, sind cytogenetische Untersuchungen von wilden, natürlichen Populationen dieser zwei Gazellenarten unentbehrlich.

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